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Russulaceae of the Pakaraima Mountains of Guyana 2. New species of *Russula* and *Lactifluus*

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Abstract— Morphological and ecological descriptions, illustrations, and taxonomic discussions are presented for a subiculate species of *Lactifluus*, *L. subiculatus,* and three species of *Russula*, *R. myrmecobroma*, *R. paxilliformis*, and *R. gelatinivelata*, all newly described from the Pakaraima Mountains of Guyana. Sequence data confirm relationships of taxa collected in Guyana within a large *Russulaceae* database.

Key Words— basidiomycetes, *Basidiomycota*, biodiversity, ectomycorrhiza, macrofungi, neotropics, *Russulales*

Introduction

A recent paper (Henkel et al. 2011) documented for the first time the sporocarp diversity of putative or confirmed ectomycorrhizal fungi in lowland tropical forests of Guyana. In that study, conducted over a ten year period from 2000 to 2010, sporocarps from 172 species of macrofungi representing 13 families and 25 genera of primarily *Agaricomycetes*, but also *Ascomycota* (*Elaphomycetaceae*), were collected from plot studies and opportunistic exploration of the *Dicymbe* (*Fabaceae* subfam. *Caesalpinioideae*) dominated forests of the Upper Potaro River Basin. Of these families, the *Russulaceae* contained the most species, many new to science.

The present communication provides macro-, micromorphological, and ecological descriptions and illustrations for four new taxa in the *Russulaceae* that contributed significantly to the biodiversity in the aforementioned plot studies (Henkel et al. 2011). Taxonomic discussions are also provided, guided by sequence analyses that will be detailed elsewhere.

Materials & methods

Collecting expeditions were made in the rainy seasons (typically May–July) 2000–2011 to the Upper Potaro River Basin along Guyana's western border with Brazil, in the south-central Pakaraima Mountains (general area: 5°05′N 59°58′W). Basidiomata were examined in the field for fresh characteristics. Color characteristics were coded according to Kornerup & Wanscher (1981; code noted in parentheses) and described subjectively. Spore deposits were taken on acetate sheets and examined for fresh color characteristics. The $FeSO_4$ macrochemical test was performed using a large mineral crystal that was rubbed directly on the stipe, lamellae and flesh. Basidiomata were dried slowly using large bead silica gel and subsequently placed in re-sealable plastic bags with small bead silica gel to prevent spoilage in the excessively humid conditions. In addition, basidiomata in various stages of development were immersed in ethanol for preservation and for molecular analysis. DNA extraction, sequencing and molecular analysis were generally those described in Miller et al. (2006).

Microscopic anatomical details were determined from dried basidiomata with an Olympus BH–2 microscope with bright-field optics and drawings were made with a camera lucida attachment. For basidiospores at least 20 individuals were observed and measured per taxon. The acid resistant reaction in basic fuchsin, the cresyl blue reaction, and the sulfovanillin reaction were prepared according to Singer (1986).

Herbaria designations are after Holmgren et al. (1990) and include: BRG – University of Guyana, Georgetown; HSU – Humboldt State University; RMS – Solheim Mycological Herbarium; LSUM – Louisiana State University Bernard Lowy Mycological Herbarium.

Taxonomy

Lactifluus subiculatus S.L. Mill., Aime & T.W. Henkel, **sp. nov.** Plates 1–2

MycoBank MB 564265

Sed Lactifluus subiculatus *atrohervolo pileo maturo et crustoso, versus gracili tomentoso stipite differt.*

Type: Guyana, Pakaraima Mountains, Upper Potaro River Basin, *Dicymbe altsonii* stand, 22.V.2000, SL Miller 10047 (**Holotype**, RMS; **isotype,** BRG; GenBank JQ405654).

Etymology: *subiculatus* (Lat.), referring to the dense subiculum from which the basidiomata arise.

Pileus 0.9–3 cm broad, at first convex, then plane to slightly depressed to irregularly infundibuliform; margin incurved and regular when young, then decurved, entire to undulating, obscurely striate at first, then irregularly subsulcate when older; extreme margin distinctly membranous for up to 1 mm; pellis finely velutinous to hispidulose or subtomentose when young, then rugulose and minutely areolate especially at the disk, tacky to slightly lubricous when moist, light brown (6D6–8) overall impression, light brown (6D6–8) to yellowish brown to golden brown (5D6–8) when young, mottled and streaked with pale to light orange (5A3–4) and less frequently with brown (6E–7) with age, with extreme margin pale orange white. Lamellae 2–3.5 mm wide at

Plate 1. *Lactifluus subiculatus* habit (Miller 10047). 1. Basidiomata produced on shaggy subiculum enshrouding base of sapling, ×1.8. 2. Stipe showing disrupted crust of pigment and minutely fluted topography, along with lamella morphology, ×2.1. 3–4. Extensive subiculum on boles of large *Dicymbe corymbosa* trees. 3. ×0.15. 4. Arrow indicates *L. subiculatus* basidiomata and cluster of primordia, ×0.2.

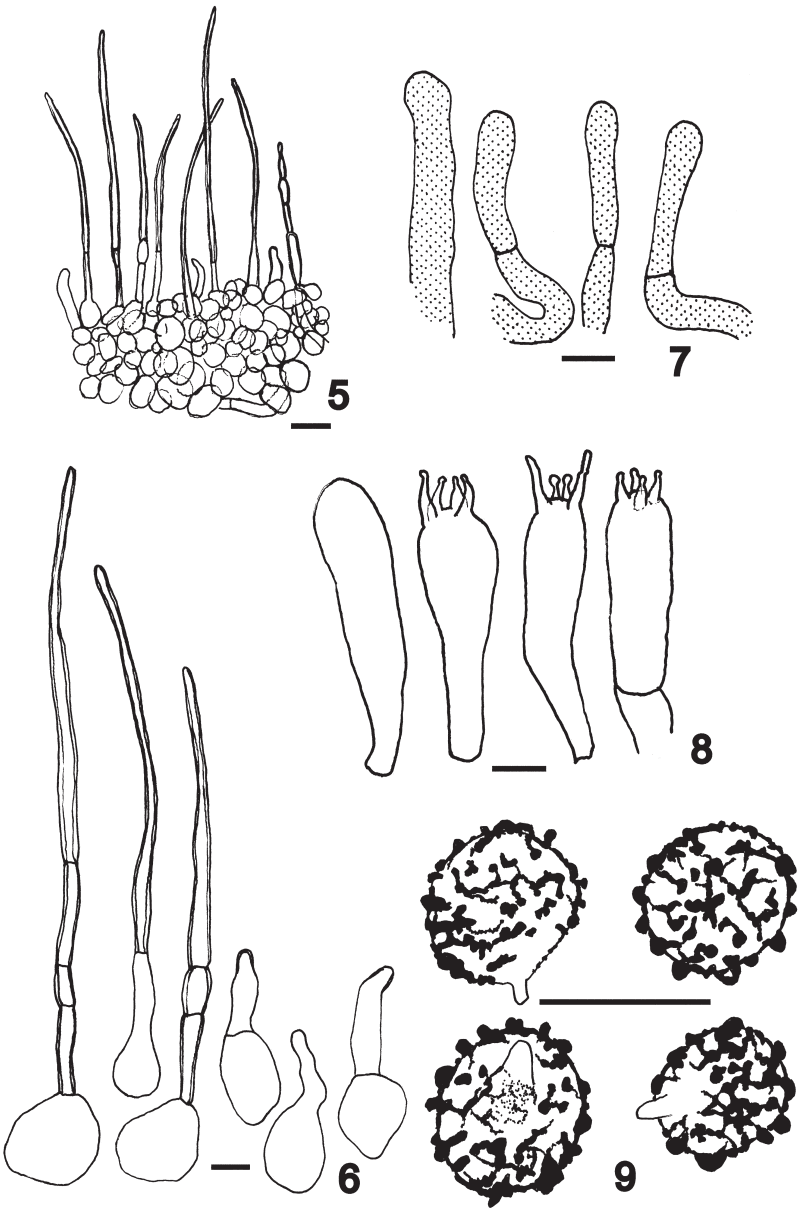

Plate 2. *Lactifluus subiculatus* (Miller 10047), microscopic features. 5. Diagram of a section of the two-layered pileipellis; the suprapellis is a lampropalisade of thick-walled hairs over a pseudoparenchymatous subpellis. 6. Elements of the suprapellis. 7. Gloeopleurous hyphae. 8. Basidia. 9. Basidiospores. Scale bars = 10 μm.

mid-radius, irregularly adnate to subdecurrent, unequal, close when young then subdistant, not or occasionally intervenose and forking, thin at first then moderately thick, rounded, white to pale yellow (4A3–4 to 5A2), unchanging; edge entire, concolorous; lamellulae of three different lengths. Stipe 4–8 × 8–15 mm, cylindrical, equal or tapered to the base, curved, attachment central, occasionally distinctly fluted, yellowish white to pale creamy tan (4A2 to 5B4–5) above, concolorous with pileus below, subvelutinous toward the base at first, then this tissue cracking into distinct isolated patches; arising from a thin, coarse, erect tomentose subiculum. Context 1–2 mm at mid-radius, firm, solid in lamellae and stipe, white, unchanging; odor strong fungal; taste disagreeable. Latex absent or scant, watery, unchanging. $FeSO_4$ quickly dull green on lamellae and trama. Subiculum usually distinct and extensive, shaggy, off-white to greyish cream, composed of fascicles of hyaline, linear hyphae or hairs 2–8 µm wide, thick-walled (≤ 2–2.5 µm).

Basidiospores 7.6–9.2(–9.6) × 6.4–7.6 µm (Q = 1.18–1.21–1.26), subglobose to short ellipsoid; ornamentation amyloid, composed of irregularly sized and shaped warts; warts 0.5–1.0 µm high, usually obtuse, isolated or connected by fine lines forming a fine partial reticulum; hilar appendix prominent, 3–4 × 1.5–2 µm, hyaline; suprahilar plage non amyloid or with faint fine reticulum, rarely with an isolated amyloid spot. Basidia clavate, 45–60 × 15–18 µm, 4–spored, sterigmata 7–9 × 1–2 µm. Pseudocystidia 5–10 µm wide, cylindrical or irregularly contorted, rounded or blunt-pointed at the apex, not emergent, infrequent to abundant, thin-walled; contents refractive granular, SV–; connected deeply to laticiferous hyphae in the trama with similar contents. Pleurocystidia absent. Hymenophoral trama irregular, composed of interwoven, hyaline, thin-walled hyphae, which are 3–5 µm diam with scattered inflated cells of 8–10 µm wide; lactiferous hyphae scattered, 8–11 µm wide with refractive guttulate contents; sphaerocytes rare or absent; subhymenial layer not well developed. Pileipellis a sparse to dense lampropalisade; elements of suprapellis 35–150(–220) × 5–10 µm, cylindrical, hair-shaped, septate, with wall 1–2 µm thick, frequently with swollen base; subpellis pseudoparenchymatous; cells isodiametric, obovate, napiform to obpyriform, 10–40 µm diam, with yellowish brown contents in KOH, cylindrical to slightly contorted; all cells SV–. Stipitipellis similar to pileipellis but hair-like elements less numerous, surface tissue often nearly occluded by external yellowish brown amorphous pigment in KOH; SV–.

Habit, habitat, and distribution – Solitary to fruiting in small numbers on lower trunks of saplings, larger trees, stumps and other elevated positions, arising from a shaggy, often deep and extensive, persistent subiculum which enshrouds living and dead objects above the surface of the ground and which is often interspersed with or overriding bryophyte growth, subtended by

ectomycorrhizal rootlets; found May through early July during wet weather in forests dominated by *Dicymbe corymbosa* and *D. altsonii*. Ectomycorrhizal associations with the leguminous hosts in Guyana were confirmed with the aid of molecular analysis (Smith et al. 2011)). Known only from the type locality in the Upper Potaro Basin of Guyana, and Mabura.

Additional specimens examined. **GUYANA. Region 8 Potaro–Sipiruni.** Pakaraima Mountains, Upper Potaro River Basin, within 5 km radius of Potaro base camp located at 5°18′04.8″N 59°54′40.4″W, 710–750 m, 17.V.2000, Miller 10010 (BRG, RMS); Miller 10021 (BRG, RMS); 28.VII.2000 Henkel 7922 (BRG; HSU). Near Ayanganna Airstrip, 16.V.2000, Miller 10004 (BRG, RMS); 20.V.2000 Miller 10034 (BRG, RMS). ***Dicymbe altsonii* stand**, 22.V.2000 Miller 10047 (BRG, RMS). *Dicymbe* Research Plots, 27.V.2000, Miller 10061 (BRG, RMS); 1.VI.2000, Miller 10087 (BRG, RMS); 3.VI.2000, Miller 10094 (BRG, RMS); 8.VI.2000 Miller 10114 (BRG, RMS). Vicinity of base camp, 28.VII.2000, Henkel 7922 (BRG, HSU); 15.V.2010 Aime 3937 (BRG, LSUM). ~3 km SE of Potaro base camp near *Dicymbe* plot 1, 25.V.2001, Henkel 8210 (BRG, HSU). 1 km SW of base camp near Blackwater point, 10.VII.2010, Henkel 9020 (BRG, HSU). Near *Dicymbe* Plot 2, 26.V.2010, Henkel 9229 (BRG, HSU). **Region 10–Upper Demerara-Berbice.** Mabura Ecological Reserve, *Dicymbe altsonii* stand, 24.V.2011 Aime 4276 (BRG, LSUM).

Commentary – Previously, three neotropical species of *Lactarius* that produce basidiomata from an extensive and well developed subiculum have been described (Singer 1984; Miller et al. 2002; Miller & Henkel 2004): *L. panuoides* Singer, *L. brunellus* S.L. Mill. et al., and *L. multiceps* S.L. Mill. et al.. *Lactarius panuoides* and *L. brunellus* are pleurotoid, while *L. multiceps* has a short, but occasionally well-developed, eccentric stipe (Miller et al. 2002). The stipe of the milkcap described here is larger and centrally attached, and the basidioma stature is typically more agaricoid than pleurotoid. Molecular data confirm that our species forms ectomycorrhizae with the leguminous hosts *D. corymbosa*, *D. altsonii*, and *Aldina insignis* in Guyana (Smith et al. 2011).

The infrageneric placement of *L. subiculatus* is unclear. It is clear that the species belongs to *Lactifluus*, which was recently split from *Lactarius* (Buyck et al. 2008, 2010; Verbeken et al. 2012). The rDNA molecular phylogenetic analysis (SL Miller, unpublished) indicates a close relationship with *Lactifluus neotropicus* (Singer) Nuytinck, originally described from Trinidad, but collected also from Guyana (SL Miller, unpublished). The combination of long thick-walled hairs in the suprapellis arising from an epithelioid subpellis (which both species share) is characteristic of several *Lactifluus* groups in both the old- and new-world tropics, including *L.* sections *Lactariopsis* Verbeken, *Chamaeleontini* (Verbeken) Verbeken, *Pseudogymnocarpi* (Verbeken) Verbeken, *Phlebonemi* (R. Heim ex Verbeken) Verbeken, and *Polysphaerophori* (Singer) Verbeken (Pegler & Fiard 1979, Singer et al. 1983, Verbeken & Walleyn 2010). Singer (Singer et al. 1983) and Pegler & Fiard (1979) differentiated sections *Lactariopsis* and *Polysphaerophori* by the presence of a partial veil or, more precisely, an annulus

or remnants of a veil on the stipe in sect. *Lactariopsis*. Similarly, Verbeken & Walleyn (2010) distinguished sect. *Lactariopsis* from sect. *Chamaeleontini* based on the presence of an annulus in the former. Sect. *Polysphaerophori* Singer, erected for South American species (Singer 1973), was used to place the African "*Gymnocarpi*" by Verbeken & Walleyn (2010), who rightly recognized the artificial distinction between several of these groups and maintained them only for practical reasons.

Macroscopically, the brownish orange colours and pilose to velutinate pileus surface, and microscopically, the abundant sphaerocytes in the hymenophoral trama, the thick-walled elements in the pileipellis, and spores with low ornamentation forming a partial to nearly complete reticulum in *L. subiculatus* are consistent with *L.* sect. *Lactariopsis*. Although *L. subiculatus* has not been observed to form a distinct annulus, the extreme margin does have a distinct flap of tissue that may be easily interpreted as the remnants of a partial veil.

The other subiculate species, *L. multiceps*, *L. brunellus* and *L. panuoides*, have not yet been recombined in *Lactifluus*. They all combine the subiculate character with a pleurotoid habit and, up to now, all pleurotoid milkcaps that have been molecularly investigated belong to *Lactifluus*.

Russula myrmecobroma S.L. Mill., Aime & T.W. Henkel, **sp. nov.** Plates 3–4

MycoBank MB 564264

Ab aliis speciebus Russulae *stipite cinereo, pileo fusco, deinde irregulariter diaphano ubi udo et fascianti in centro propriam ordinationem reticulatam, ordinate dispositis striis pro longitudine aequalibus, lamellis aggregatis et sapore acris differt.*

Type: Guyana, Pakaraima Mountains, Upper Potaro River Basin, near Hogback Ridge, 5.VI.2000, SL Miller 10109 (**Holotype**, RMS; **isotype**, BRG; GenBank JQ405657).

Etymology: *myrmecobroma* (Gk.), literally ant food, referring to the regular dismemberment of the basidiomata by ants.

Pileus 3.5–4.5 cm broad, broadly convex at first, then plane and finally depressed; margin entire when young, then undulating, obscurely striate at first, then with regularly spaced and sized striations; striations 2 mm long; pellis dull, dry, smooth at disk, frequently pruinose at mid-radius and at margin, yellowish brown (5E–F–8 to 5D–E 5) overall at first, becoming hygrophanous with irregular reticulate pattern especially halfway the radius and with color fading to dark blond (5C–4, 5C–D–3) to orange grey (5B–2) with irregular areas of 5B–3–5; disk and margin not hygrophanous and usually remaining darker. Lamellae 1–2 mm broad at mid-radius, adnate, sinuate or slightly subdecurrent, crowded, forked at stipe and occasionally elsewhere, arising at different positions relative to the stipe giving uneven appearance, pallid cream (near 4A–2), becoming spotted with yellow or reddish brown where injured; lamellulae present, 4–5 ranked; edge entire. Stipe 3–5.7 × 0.8–1.1 cm, equal to subclavate or tapering to the base, centrally attached, moderately distinct

Plate 3. *Russula myrmecobroma* habit. 10. Bisected basidiome (Miller 10109), ×1.1. 11. Basidiome (Miller 10161) exhibiting damage by ants (arrow), ×1.2.

longitudinal ridges beneath felted subtomentose covering especially below, tomentum white to pale grey (5A–B–1), pale orange grey (5B 2–3) beneath, grey brown where handled and where longitudinal ridges become exposed. Context in pileus 2–2.5 mm at mid-radius, stuffed pallid grey cream; context in stipe cylinder whitish marbled with pale grey, turgid to pliant, pallid cream to pale grey brown, discoloring pale orange or orange brown where injured; odor sharp acrid heading toward latex paint; taste strongly acrid; $FeSO_4$ quickly salmon on stipe surface and trama.

Basidiospores 6.4–7.2(–8) × 5.6–6.8 µm (Q = 1.05–1.14–1.17), subglobose to broadly ellipsoidal; ornamentation reticulate, consisting of low blunt spines, 1–1.3 µm high, connected by fine lines or verrucae, strongly but often partially amyloid; suprahilar plage not distinct to finely reticulate. Basidia 55–62 × 12–15 µm, subclavate to nearly cylindrical, 4–spored; sterigmata stout 7–10 × 2–3 µm. Cystidia 80–95 × 15–20 µm, subclavate to subfusiform, thin or thick walled, emergent for ca. 20–30 µm, numerous, arising from gloeopleurous elements, with refringent to crystalline contents, SV+, thick walled lamprocystidia present but not numerous. Marginal cells 55–105 × 8–15 µm, narrowly subclavate, tortuous, thin-walled, optically empty, abundant. Subhymenium distinct, a gelatinous layer composed of interwoven cylindrical flattened and variously swollen hyphae of 2–5 µm diam. Lamellar trama with large sphaerocytes and scattered hyphae, with gloeopleurous fragments and embedded dermatocystidia near the pileus. Pileipellis orthochromatic in Cresyl Blue, two-layered; subpellis gelatinized, forming a dense mat close to the underlying trama, of tightly interwoven hyphae; hyphae 2–5 µm diam, thin-walled, frequently septate, with scattered strongly refringent gloeopleurous elements of 5 µm diam, frequently terminating with cylindrical to swollen or mucronate

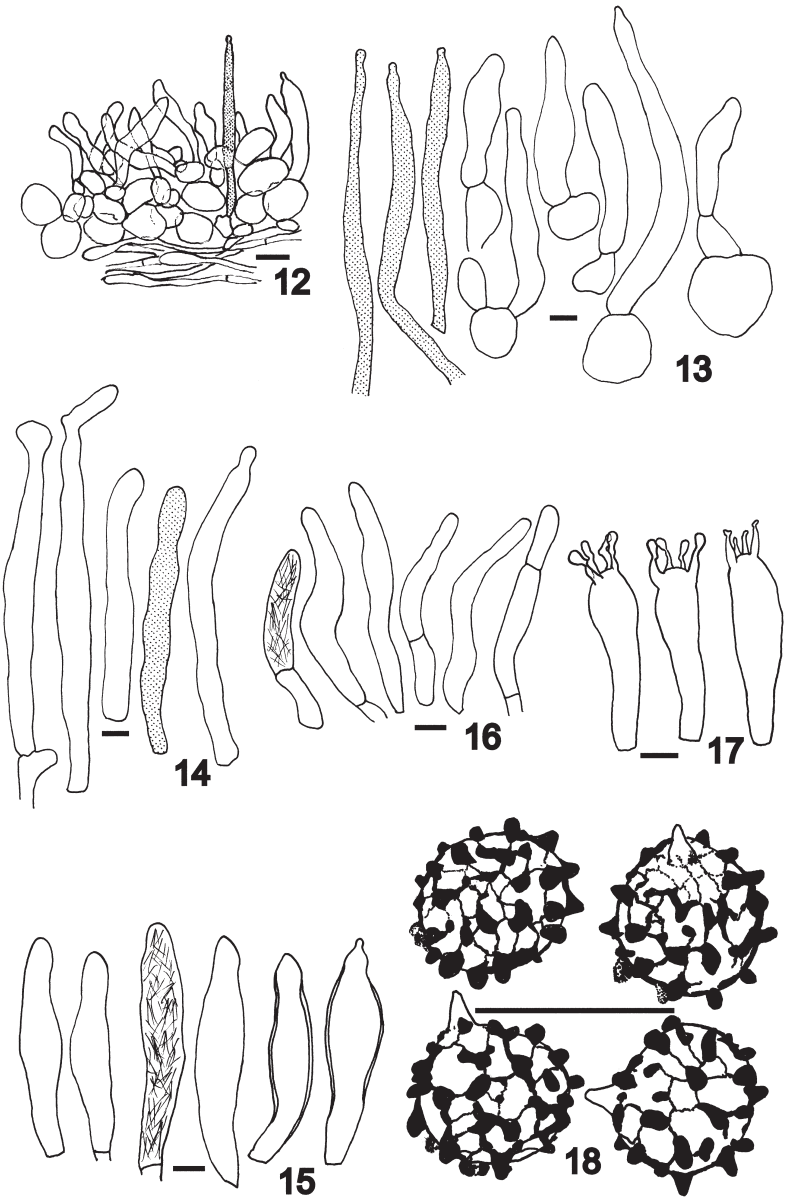

Plate 4. *Russula myrmecobroma* (Miller 10109), microscopic features. 12. Diagram of a section of the two-layered pileipellis; the suprapellis is a trichodermial palisade over a thin pseudoparenchymatous subpellis. 13. Elements of the suprapellis. 14. Elements of the stipitipellis. 15. Hymenial cystidia. 16. Marginal cells. 17. Basidia. 18. Basidiospores. Scale bars = 10 μm.

embedded dermatocystidia; suprapellis composed of 2–5 strongly inflated, spherical cells, often gradually smaller towards the terminal cell, the latter cylindrical to narrowly subclavate, ampullaceous, or mucronate, resembling an epithelium; pileocystidia dispersed, terminal, more or less the same diam. as other terminal elements, 50–90 × 10–13 µm, contents granular-refringent in KOH. Stipitipellis a turf of variously shaped caulocystidia, 100–170 × 9–14 µm, these narrowly cylindrical, mucronate, capitate or tortuous.

Habit, habitat, and distribution – Solitary or fruiting in small numbers on root mats of the ECM trees *Dicymbe corymbosa*, *D. altsonii*, *D. jenmanii, Aldina insignis* and *Pakaraimaea dipterocarpacea*, widespread in the Pakaraima Mountains but not common; found May through early July during wet weather and also in December–January. Known from Mabura Hill and the Upper Potaro and Upper Mazaruni River Basins of Guyana.

Additional specimens examined: **GUYANA. Region 8 Potaro–Sipiruni.** Pakaraima Mountains, Upper Potaro River Basin, within 15 km radius of Potaro base camp located at 5°18′04.8″N 59°54′40.4″W, 710–750 m. Vicinity of Potaro Base Camp, 21.V.2000, Miller 10045 (BRG, RMS); 24.VI.2000, Miller 10161 (BRG, RMS). ~3 km SW of base camp near *Dicymbe* plot 3, 8.VI.2001 Henkel 8258 (BRG; HSU). 1 km SW of base camp near Blackwater point, 10.VII.2009, Henkel 9016 (BRG; HSU). 15 km east of Potaro base camp near Tadang base camp, in mixed *Dicymbe corymbosa–Dicymbe altsonii–Aldina insignis* forest, 24.XII.2009, Henkel 9145 (BRG; HSU). *Dicymbe* plot 1, 5.VI.2001, Aime 1783 (BRG, LSUM); 15.V.2010, Aime 3935 (BRG, LSUM). *Dicymbe* plot 2, 6.VI.2001, Aime 1823 (BRG, LSUM). **Region 7 Cuyuni–Mazaruni.** Pakaraima Mountains, within 1 km radius of Piegaimah base camp at 5°26′21.3″N 60°04′43.1″W. Vicinity of base camp, in savanna fringing forest under *Pakaraimaea dipterocarpacea* and *Dicymbe jenmanii*, 24.XII.2010, Henkel 9523 (BRG; HSU). ~1 km SW of base camp, in stand dominated by *Pakaraimaea dipterocarpacea* and lacking *Dicymbe jenmanii*, 26.XII.2010, Henkel 9546 (BRG; HSU). **Region 10–Upper Demerara-Berbice.** Mabura Ecological Reserve, *Dicymbe altsonii* stand 1, 1.VI.2011, Aime 4360 (BRG, LSUM).

Commentary – It is relatively difficult to find fresh basidiomata of *R. myrmecobroma* that have not been extensively damaged by ants. While ants will disarticulate and carry off pieces of a variety of fungal fruiting structures, they seem to be especially attracted to *R. myrmecobroma*, and in Guyana only *R. batistae* Singer seems to be more attractive. Microscopically both fungi appear to have relatively primitive traits such as an abundant gloeoplerous system with embedded dermatocystidia in the pileipellis and abundant macrocystidia of two types deeply rooted in the hymenium, all strongly positive in sulfovanillin. Both also have an acrid to strongly acrid taste. It is unknown whether any of these characteristics serve as an attractant to the ants.

From an ecological standpoint, *R. myrmecobroma* may be a quite important mycorrhizal symbiont in Guyana's *Dicymbe* forests. In a recent study by Smith et al. (2011) in the Upper Potaro Basin, *R. myrmecobroma* was the most frequently ECM fungus out of 118 taxa recovered by molecular methods on

ECM roots of 19 trees each of three sympatric host species, *D. corymbosa*, *D. altsonii*, and the papilionoid *Aldina insignis*. In a second study (ME Smith & TW Henkel, unpublished) investigating mycorrhizal symbionts of the ECM dipterocarp, *Pakaraimaea dipterocarpacea,* and the sympatric *Dicymbe jenmanii* in the Upper Mazaruni Basin, *R. myrmecobroma* was the sixth most common mycobiont recovered among about 50 species of EM fungi associated with 20 trees of each host species, indicating a broad host and distribution range for the fungus in Guyana. It is interesting to speculate that movement of tissue pieces by the ants might contribute to the frequency of *R. myrmecobroma* in the forest.

Molecular analysis (SL Miller, unpublished) indicates a close relationship between *R. myrmecobroma* and *R. batistae*, despite the fact that macroscopically they are very different. *Russula batistae* has irregular, broad, subdistant to distant lamellae, no lamellulae, and a deeply sulcate pileus margin, while *R. myrmecobroma* has regular, rather narrow, crowded lamellae, abundant lamellulae, and a regularly short-striate margin. Singer erected *R.* subsect. *Batistinae* in the large section *Pellicullariae* to accommodate *R. batistae*. This subsection likely will not suffice as no velar tissue has been observed in *R. myrmecobroma*, suggesting a need to refine the description of the subsection. Buyck (1990a) has shown that *R.* sect. *Pellicullariae* is highly heterogeneous and possibly not monophyletic, indicating the possible need for a new infrageneric group at the sectional level to accommodate *R. batistae* and *R. myrmecobroma*.

Russula paxilliformis S.L. Mill., Aime & T.W. Henkel, **sp. nov.** Plates 5–6

MycoBank MB 564266

Pagina pilosa rupenti in fine squamellas tenues prope marginem, exponenti texturam pallidam et stipitem velutinum basin versus decrescentem et sine profunde striato margine.

Type: Guyana, Pakaraima Mountains, Upper Potaro River Basin, vicinity of Potaro Base Camp, 3.VI.2000, SL Miller 10097 (**Holotype**, RMS; **isotype,** BRG; GenBank JQ405656).

Etymology: *paxilliformis* (Lat.), referring to the pilose pileus with inrolled margin and coloration reminiscent of *Paxillus involutus*.

Pileus 3–8.5 cm broad, convex at first with deeply depressed disk, becoming plane or uplifted, often with a hole entirely through the disk of the pileus where ants have eaten away the tissue; margin tightly inrolled around stipe at first with a frail tomentose partial veil connecting margin to stipe, in age margin becoming separated, then decurved, and finally plane leaving no annulus or other trace of a veil, entire, not striate when young, becoming obscurely striate with age; pellis dull, dry, densely subtomentose to velutinous when young, concentrically cracking to become areolate, granulose to squamulose,

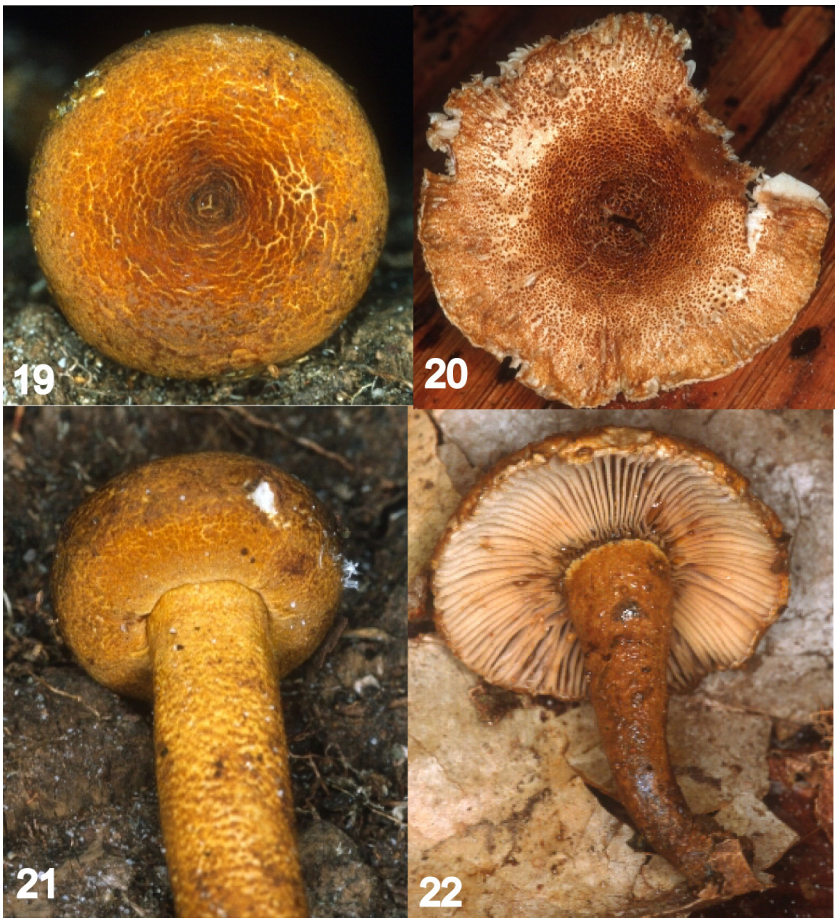

Plate 5. *Russula paxilliformis* habit. 19. Top surface of unexpanded pileus showing radial cracking of pilose pellis (Miller 10097), ×1.8. 20. Top surface of expanded pileus showing radial cracking at the disk and areolate or granulose texture near the margin (Miller 10097), ×0.8. 21. Side view of unexpanded pileus showing tightly inrolled and pale colored margin, and subtomentose and ornamented stipe (Miller 10097), ×1.8. 22. Mature basidiome with partially expanded pileus showing velar remnants at the margin, and subtomentose stipe (Miller 10070), ×0.9.

remaining so especially at the disc; pileus and partial veil light brown to golden brown (5C–D 6–7) overall, disk yellowish brown (5D6–8) when young, with an orange white subcutis (near 5A–2) showing through, with age areoles (?) darkening to brown (6E 7–8) with orange white 5A–2 or light brown (near 6D4–5) showing through, disk brown (6–7 E 6–7). Lamellae 3–4 mm broad at mid-radius, adnate to slightly decurrent, close, rarely forking at stipe and

elsewhere, entire, firm when young, soft with age, whitish to cream, discoloring pale reddish brown where handled; lamellulae absent. Stipe 5.5–8 × 0.9–1.0 cm, cylindrical to tapering to the base when young, strongly tapering to the base and often flared at the apex in age, usually with a pronounced depression around stipe apex where tightly inrolled pileus and partial veil were connected, commonly curving, attachment central, even, highly tomentose to scurfy, with more or less concentric areolate stretch marks when older, matted to flocculose where handled; light brown to golden brown (5 C–5–7 to 5D–5–8), at first areolae yellow brown (5E–8, with age 5E–6–7), over light brown (5C–5–6) ground beneath, then yellowish white to pale creamy tan (4A2 to 5B4–5) above, light brown to brown (5–6D –6–7) or dark brown (6F5–6) below. Context in pileus 2.5–3 mm at mid-radius, firm at first, then soft, pallid cream; trama in stipe with distinctive anatomy in longitudinal section, with a discrete separable cylinder-like plug of hard tissue forming a central core from pileus in upper two thirds of the stipe, surrounded by firm tissue comprising most of the stipe, outer cylinder marbled bluish steel gray from base over lower one-half, in older specimens the central core has frequently been completely eaten away by ants so that the stipe is hollow; odor strongly fungal, like *Scleroderma;* taste disagreeable at first, then slowly acrid; $FeSO_4$ quickly salmon on stipe trama.

Basidiospores (6.8–)7.2–7.46–8 × 6–6.8(–7.2) µm (Q = 1.06–1.13–1.27), subglobose to broadly ellipsoidal; ornamentation reticulate or incompletely reticulate; ornamentation consisting of partial crests with short lateral diverticulations and large broadly conical or multiplex blunt spines, 1.6–2.8 µm high, connected by fine lines or verrucae, strongly but often partially amyloid; suprahilar plage moderately large, verruculose, barely decurrent on apiculus. Basidia 50–65 × 12–15 µm, subclavate to subcylindrical, 4-spored; sterigmata 8–10 × 1–3 µm. Cystidia 70–95 × 6–13 µm, cylindrical to subfusiform, obtuse, deeply rooting, mostly thin-walled, emergent 30–35 µm above basidia, SV+, contents crystalline, numerous. Marginal cells 65–105 × 10–18 µm, cylindrical to subfusiform, SV+, numerous. Trama of lamellae and pileus composed of large well-developed nests of sphaerocytes; subhymenium not well developed. Pileipellis orthochromatic in Cresyl Blue, two-layered; subpellis of loosely interwoven hyphae of 4–5 µm diam. with scattered gloeoplerous elements of 5 µm diam., pale brownish grey in SV; suprapellis a dense trichoderm of digitate, septate hyphae; terminal elements cylindrical, obtuse, often sinuous, 20–60 × 2.5–5 µm, occasionally thick-walled, arising from long chains of spherical to irregularly shaped cells, evenly brown in KOH, interior walls irregularly thickened and jagged; pileocystidia 25–60 × 3–6 µm, narrow cylindrical, obtuse to subcapitate, rare or absent; all elements SV–, encrustations highly acid resistant in basic fuchsin, dark purple, abundant. Stipitipellis a dense trichoderm similar to the suprapellis,

composed of long chains of cylindrical, spheroidal to irregularly shaped cells, terminated by brownish ellipsoid or pyriform cells, internal walls irregularly thickened; cystidia rare or absent.

Habit, habitat, and distribution – Solitary to widely scattered on root mats of *Dicymbe corymbosa*, uncommon; found May through early July during wet weather. Known only from the type locality in the Upper Potaro Basin of Guyana.

Additional specimens examined: **GUYANA. Region 8 Potaro–Sipiruni.** Pakaraima Mountains, Upper Potaro River Basin, within 5 km radius of Potaro base camp located at 5°18′04.8″N 59°54′40.4″W, 710–750 m. Near Ayanganna Airstrip, 20.V.2000, Miller 10039 (BRG, RMS). *Dicymbe* Research Plots, 27.V.2000, Miller 10070 (BRG, RMS). Vicinity of Potaro Base Camp, 31.V.2001, Aime 1724 (BRG, LSUM). ~3.5 km SE of base camp near *Dicymbe* plot 2, 12.VI.2001, Henkel 8270 (BRG; HSU); 19.V.2010 Aime 3974 (BRG, LSUM). Mixed Forest Research Plots MP1, 7.VII.2009, Henkel 9006 (BRG, HSU). Near Potaro Falls, 4.VII.2002, Aime 2196 (BRG, LSUM).

Commentary – This is an unusual *Russula* species whose initial encounter in the low-tech environment of field work in Guyana sparked a great deal of debate regarding generic placement. The combination of pilose pileus, strongly inrolled margin, somber yellowish brown to dull brown colors, and tendency for the lamellae and stipe to discolor brownish, was reminiscent of the temperate *Paxillus involutus*. However, close observation of the basidiospores in Melzer's reagent, even without a microscope, confirmed the amyloid reaction.

Molecular analysis (SL Miller, unpublished) places *R. paxilliformis* consistently near *R. matoubensis* Pegler. *Russula matoubensis* is a much brighter orange but also has a subtomentose (especially when collected fresh in dry conditions) pileus that becomes finely granular to areolate-disrupted and squamulose away from the disc, exposing the underlying and much lighter colored tissue beneath. Microscopically, both fungi also possess a trichodermial palisade in the pellis, composed of ascendant hyphae, rare dermatocystidia and interwoven hyphae in the subpellis that are heavily encrusted with material that is positively acid resistant in basic fuchsin. In both fungi, scalp sections of the pileus cuticle turn instantly dark brown in KOH. Also, both taxa contain subpellis cells with irregularly thickened cell walls and lamprocystidia in the hymenium.

Pegler & Fiard (1979) placed *R. matoubensis* in *R.* sect. *Decolorantinae* Meltzer & Zvara based on orange pigment, mild taste, white context that discolors grey, and the presence of dermatocystidia in the pellis. Singer et al. (1983) acknowledged possible placement in *R.* subsect. *Decolorantes* (= *Decolorantinae*) but, noting the close resemblance of the anatomical characters to those of *R. fistulosa* R. Heim, ultimately placed *R. matoubensis* into subsect. *Fistulosinae* R. Heim ex Sing. Indeed, our molecular analysis consistently supports *R. paxilliformis* and *R. matoubensis* as a sister group to a clade

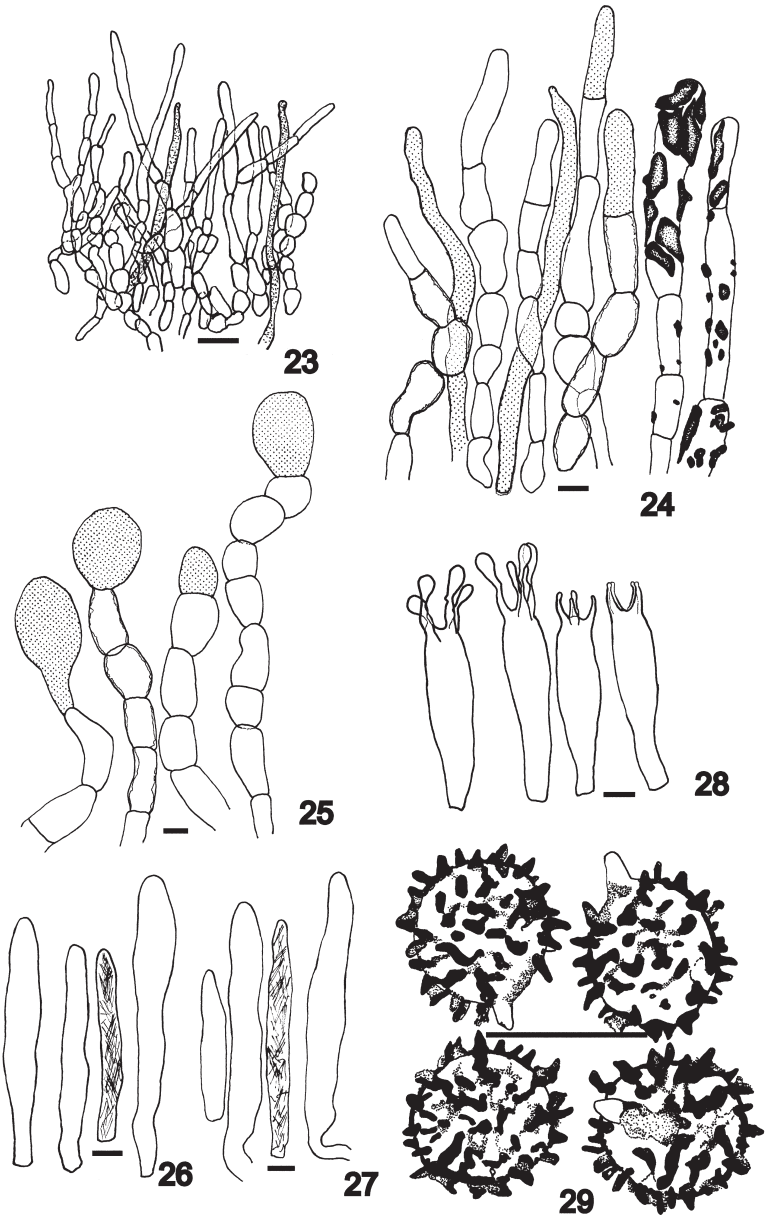

Plate 6. *Russula paxilliformis* (Miller 10097), microscopic features. 23. Diagram of a section of the dense trichoderm comprising the suprapellis. 24. Elements of the suprapellis showing long narrow pileocystidia, catenulate hyphae and acid resistant encrustations. 25. Elements of the stipitipellis. 26. Hymenial cystidia. 27. Marginal cells. 28. Basidia. 29. Basidiospores. Scale bars = 10 µm.

containing *R. ochraceorivulosa* Buyck, which Buyck (1994a) placed into subsect. *Pallidorimosinae* Buyck, and *R. patouillardii* Singer, which Buyck (1994b) placed into subsect. *Virescentinae* Singer. Morphologically, *R. paxilliformis* appears similar to members of the African subsections *Brunneofloccosinae* (e.g., *R. aurantiofloccosa* and *R. brunneofloccosa*) or *Testaceoaurantiacinae* (e.g., *R. testaceoaurantiaca* Beeli or *R. binganensis* Beeli), both described by Buyck (1990b). The features common to both the South American and African species are the abundant catenulate chains of spherical to cylindrical highly encrusted cells in the pellis, the pilose to velutinous pileus that develops a distinctive radial cracking pattern toward the margin, the basidiospores with fine connectives between amyloid ornamentation elements and frequently a large amyloid plage, and flesh or stipe surface that discolors brownish.

Russula gelatinivelata S.L. Mill., Aime & T.W. Henkel, **sp. nov.** Plates 7–8

MycoBank MB 564267

Distincto gelatinoso partiali velo circa pileum et inferam partem stipitis juniorum, piloso rubrobrunneo pileo, et stipite cum rubra pilosa pagina in medio in distinctam areolatam ordinationem frangatur differt.

Type: Guyana, Pakaraima Mountains, Upper Ireng River Basin, east bank of Ireng River, 1 km downstream from Kurutuik Falls in *Dicymbe*-dominated slope forest, 15.V.1998, TW Henkel 6410 (**Holotype**, HSU; **isotype,** RMS, BRG; GenBank JQ405655).

Etymology: *gelatinivelata* (Lat.), referring to the gelatinous partial veil evident in young, fresh specimens.

Pileus 5.5 cm broad, convex at first, then broadly convex to slightly depressed; margin incurved at first, then decurved, entire when young, then frequently lacerate with age, obscurely striate when young, tuberculate striate when older, striations 6 mm in length; pellis dull to shiny, with a thick gelatinous partial veil present when young with material compacted into cavity formed by margin and stipe, subvelutinous in age, violet brown (11F7–8) with extreme margin cream (3A–2) when young, then reddish brown (9–10D–E–8) to brownish violet (11E6–7) or violet brown (10F–8), disk violet brown 10–11F6–8 or occasionally with pale yellow centrally, older specimens fading to grayish red (9C–D–5–6) with disk concolorous to violet brown (10F–8). Lamellae 3–3.5 mm broad at mid-radius, adnate to slightly sinuate to subdecurrent, close, frequently forking at stipe, entire, pale yellow (3A 2–3); lamellulae absent. Stipe 4.5 × 1.3 cm, equal or more typically tapered to base, attachment central, even to slightly irregular, viscid to gelatinous over lower one-half when young, becoming subtomentose above, conspicuously areolate below, with a white to cream (3A 2–3) zone at apex (i.e. concolorous with lamellae), rarely with a pinkish tinge, middle portions overlain with grayish- to brownish-red (10D 5–7) areolae frequently in a stretch-mark like pattern over a white or yellowish white (3A2) ground; the base concolorous with the apex or yellowish white

Plate 7. *Russula gelatinivelata* habit (Henkel 8233). 30. ×0.9.

(3A2). Context in pileus 2–3 mm at mid-radius pliant, white, pale pink immediately below cuticle, especially at disk; trama in stipe stuffed at maturity, outer cylinder pale yellow surrounding white central core; odor fragrant like Avon hand lotion; taste slightly bitter; $FeSO_4$ yellow on stipe surface, quickly salmon red on trama.

Basidiospores 6.8–7.6 × 6–6.8 (Q = 1.11–1.13), subglobose to broadly ellipsoid; ornamentation of widely distributed, isolated, acute, narrowly conical elements, 1.5(–2) µm high, amyloid, darkest near the apiculus; suprahilar plage large and verruculose, not or slightly decurrent on the apiculus. Basidia (24) 28–32(–36) × 8–13 µm, clavate to subcylindrical, 2-, 3-, or 4-spored, sterigmata long, 6.4–8 × 1–1.6 µm. Cystidia 75–130 × 15–18 µm, subclavate to cylindrical, obtuse to capitate, thin-walled, some long, arising deep within the lamella trama, others shorter, arising in hymenium, emergent 10–40 µm above basidia, scattered to numerous, SV–. Marginal cells 85–95 × 15–20 µm, fusiform, mucronate, strongly emergent, mixing with small basidia, numerous. Subhymenium well developed of small tightly packed spherical cells of 10 µm diam. Lamellar trama composed of many large sphaerocytes, and nests of relatively small, nearly isodiametrical to globose sphaerocytes, interwoven with cylindrical hyphae. Pileipellis orthochromatic in Cresyl Blue, two-layered; subpellis of slightly gelatinized interwoven hyphae of 4–5 µm diam intergrading with discrete regularly spaced rosettes, these often encrusted with reddish brown pigment in KOH; suprapellis a loose trichoderm composed of frequently branching spindly hyphae; these 5–12 µm diam, cylindrical to clavate, obtuse and often sinuous and irregularly constricted, often multi-septate, thin- or exceptionally thick-walled, arising from large

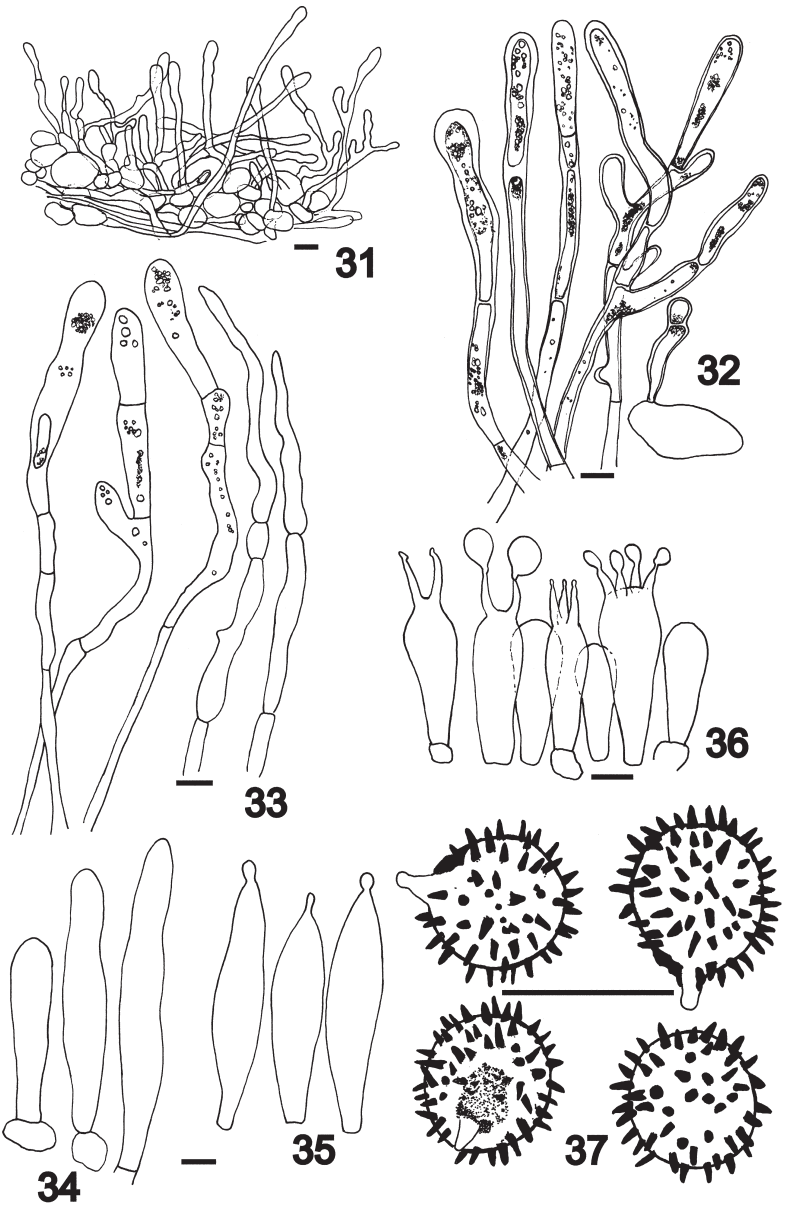

Plate 8. *Russula gelatinivelata* (Miller 10066), microscopic features. 31. Diagram of a section of the two-layered pileipellis; the suprapellis is a trichoderm over a thin pseudoparenchymatous subpellis. 32. Elements of the suprapellis. 33. Elements of the stipitipellis. 34. Hymenial cystidia. 35. Marginal Cells. 36. Basidia. 37. Basidiospores. Scale bars = 10 μm.

inflated spherical cells 2–6 deep that in aggregate resemble an epithelium; these easily disarticulated in microscopic preparations; cystidia 50–100 µm, long pedicellate, septate, irregularly constricted or swollen at the septum, thin- or thick-walled, arising deep in the trama, SV–, the contents or interior of the walls acid resistant in basic fuchsin. Stipitipellis resembling the pileipellis, composed of branching, septate, digitate to irregularly shaped hyphae that taper at the apex, and pedicellate, septate, thick-walled hyphae that are cylindrical, clavate, obtuse and irregularly constricted.

Habit, habitat, and distribution — Solitary to usually gregarious on root mats of *Dicymbe corymbosa*, or in stands of *Dicymbe altsonii* lacking *D. corymbosa*; common and widespread; found May through early July during wet weather. Known from the Upper Ireng and Upper Potaro Basins of Guyana.

Additional specimens examined: **GUYANA. Region 8 Potaro–Siparuni.** Pakaraima Mountains, Upper Ireng River Basin, elevation 710–850 m. Suruwabaru Creek, 1 km upstream of juncture with Yuarka Creek, in *Dicymbe*-dominated riparian forest, 2.III.1997, Henkel 6269 (BRG; HSU). East bank Ireng River near Sandhill Village, under *Dicymbe altsonii* in riparian forest, 1.V.1998, Henkel 6360 (BRG; HSU). East bank of Sukabi River, 1.5 km upstream from Juncture with Ireng River in *Dicymbe corymbosa*-dominated slope forest, 22.V.1998, Henkel 6441 (BRG; HSU). Toe slopes of Mt. Kukuinang, 3 km east of confluence of Sukabi and Ireng Rivers in *Dicymbe corymbosa*-dominated slope forest at 850 m elevation, 23.V.1998, Henkel 6550 (BRG; HSU). East bank of Ireng River near Sukabi camp, under *Dicymbe corymbosa*, 27.V.1998, Henkel 6638 (BRG; HSU). ~1 km east of confluence of Sukabi and Ireng Rivers, in slope forest dominated by *Dicymbe altsonii* lacking in *Dicymbe corymbosa*, 27.V.1998, Henkel 6750 (BRG; HSU). Pakaraima Mountains Upper Potaro River Basin, within 5 km radius of Potaro base camp located at 5°18′04.8″N 59°54′40.4″W, 710–750 m. Vicinity of Potaro Base Camp, 20.V.2000, Miller 10066 (BRG, RMS). *Dicymbe* stand on Benny's ridge near Potaro River camp, 11.VI.200, Miller 10125 (BRG, RMS). ~3.5 km SE of base camp near *Dicymbe* plot 2, 26.V.2010, Henkel 9226 (BRG; HSU). ~3 km SE of base camp in *Dicymbe* plot 1, 30.V.2001, Henkel 8233 (BRG; HSU). Vicinity of *Dicymbe* plot 3, 21.VI.2002, Aime 2096 (LSUM, HSU).

Commentary – Young basidiomata of *R. gelatinivelata* in moist conditions are encased in a thick gelatinous layer around the lower portion of the stipe and pileus that is present as a veil in the space between the stipe and inrolled pileus margin. The red tomentum and striped areolate patches in the middle portion of the stipe overlaying yellow ground are remarkable.

Molecular analysis (SL Miller, unpublished) indicates that *R. gelatinivelata* has a closer relationship with *Russula* temperate species than any other species collected in Guyana. Specifically there appears to be a consistent relationship with *R. nauseosa* (Pers.) Fr., *R. cessans* A. Pearson, and *R. laricina* Velen., or with *R. aurea* Pers. and *R. romellii* Maire, all temperate taxa that have large, abundant multiseptate cystidiate hyphal elements in the pellis. In *R. gelatinivelata* the walls of these elements, while not encrusted per se, are highly positive for acid resistant coloration in basic fuchsin. The temperate taxa appear to lack this

characteristic, although taxa that have been placed in closely related sections and subsections (e.g. section *Incrustatae* Romagn.) are also highly positive for acid resistant coloration in basic fuchsin, but this is expressed in the form of abundant encrustations on the exterior of the elements. *Russula gelatinivelata*, along with *R. nauseosa* and *R. laricina*, has spores with isolated elements, while *R. cessans*, *R. aurea*, and *R. romellii* have spores with at least a partial reticulum.

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